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Original Research Article

The scaling relationships of leaf biomass vs. leaf surface area of 12 bamboo species



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ABSTRACT

There is convincing evidence for a scaling relationship between leaf dry weight (*DW*) and leaf surface area (*A*) for broad-leaved plants, and most estimates of the scaling exponent of *DW* vs. *A* are greater than unity. However, the scaling relationship of leaf fresh weight (*FW*) vs. *A* has been largely neglected. In the present study, we examined whether there is a statistically strong scaling relationship between *FW* and *A* and compared the goodness of fit to that of *DW* vs. *A*. Between 250 and 520 leaves from each of 12 bamboo species within 2 genera (*Phyllostachys* and *Pleioblastus*) were investigated. The reduced major axis regression protocols were used to determine scaling relationships. The fit for the linearized scaling relationship of *FW* vs. *A* was compared with that of *DW* vs. *A* using the coefficient of determination (i.e., r^2). A stronger scaling relationship between *FW* and *A* than that between *DW* and *A* was observed for each of the 12 bamboo species investigated. Among the 12 species examined, five had significantly smaller scaling exponents of *FW* vs. *A* compared to those of *DW* vs. *A*; only one species had a scaling exponent of *FW* vs. *A* greater than that of *DW* vs. *A*. No significant difference between the two scaling exponents was observed for the remaining 6 species. Researchers conducting future studies might be well advised to consider the influence of leaf fresh weight when exploring the scaling relationships of foliar biomass allocation patterns.

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1. Introduction

Numerous studies have shown that leaf area is closely associated with the ability of plants to intercept light and is an important functional trait that can influence plant biomass allocation patterns and community dynamics (e.g., Gifford et al.,

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1984; Koester et al., 2014). Other studies have shown that leaf dry weight (DW) manifests a linear or non-linear relationship with respect to leaf surface area (A): $DW = \beta A^\alpha$, where the scaling exponent (α) can equal unity or deviate from it (e.g., Milla and Reich, 2007; Niklas et al., 2007; Sun et al., 2017), with most estimates of $\alpha > 1$ (Milla and Reich, 2007; Niklas et al., 2007). It is easy to show that the derivative of A with respect to DW is proportional to the power $(1/\alpha - 1)$ and that when $\alpha > 1$ it follows that $1/\alpha - 1 < 0$ (Niklas et al., 2009). Under these circumstances, increases in leaf surface area fail to be proportional to increases in leaf dry mass, a phenomenon referred to as “diminishing returns” (Niklas et al., 2007; Sun et al., 2017).

The goal of this study was to determine whether leaf fresh weight (FW) scales with respect to A in a similar manner to how DW scales with respect to A . Owing to the differences of foliar water content at different developmental stages (van de Sande-Bakhuyzen, 1928), FW is not necessarily a good representative of leaf biomass. Therefore, the scaling relationship of FW vs. A has been largely ignored. Yet, Weradugage et al. (2015) have reported that, over long periods of time, water uptake within leaves synchronizes with increasing leaf weight and thus they speculated that the relationship between water content and dry weight might be relatively constant. Along these lines, Shi et al. (2015) reported statistically robust scaling relationships between FW and A for four species of the genus *Indocalamus* (subfamily Bambusoideae, Poaceae). Lin et al. (2018) further showed that there is a scaling relationship between FW and A for the pooled data of 11 bamboo species, and Huang et al. (2019) showed that the scaling relationship of FW vs. A is stronger than that of DW vs. A for data sets of 15 species within the Lauraceae, Oleaceae and Poaceae. In addition, they found that the estimate of the scaling exponent of FW vs. A was numerically less than that for DW vs. A . These and other studies indicate that leaf fresh weight should not be neglected when exploring the scaling relationships among important leaf functional traits.

In this study, we used data of 12 bamboo species (6 species within the genus *Phyllostachys* and 6 species within *Pleioblastus*) to examine: (i) whether DW is proportional to FW , i.e. whether the increase of foliar water content keeps pace with the increase of DW , (ii) whether there is a scaling relationship between FW and A , (iii) whether it is stronger than the scaling relationship of DW vs. A , and (iv) whether there is a significant difference between the scaling exponent of FW vs. A and that of DW vs. A . These questions, which had not been well solved by former studies, were examined at the individual species level and at the genus level in the present study.

2. Materials and methods

2.1. Leaf collection information

Healthy and mature leaves of twelve bamboo species within two genera (*Phyllostachys* and *Pleioblastus*) were collected from the Nanjing Forestry University campus, Nanjing, Jiangsu Province, P.R. China ($32^\circ 4' 47''\text{N}$, $118^\circ 49' 2''\text{E}$) from early May to late June 2018 (Table 1). The plants had been growing on the campus for at least six years, and had experienced the same climatic conditions, which helped reduce the effects of climatic differences on leaf functional traits. For each bamboo species, ≥ 250 leaves were randomly collected from 10 individual plants. Detailed information about collection protocols are provided by Huang et al. (2019).

2.2. Measures of leaf functional traits

Each leaf was scanned and images were saved as bitmap images at a 600-dpi resolution using an Aficio MP 7502 scanner (Ricoh, Tokyo, Japan). Adobe Photoshop (version: CC, 2017) was used to obtain a leaf profile in a black and white image. The protocols described by Shi et al. (2018) and Su et al. (2019b) were used to measure leaf length, width, and area. Leaf length was defined as the distance between leaf apex and leaf base that is at the junction of the blade and the petiole. Leaf width was defined as the maximum distance between two points on the edge of the blade that is perpendicular to the straight line through leaf apex and leaf base. Turgid leaves were weighed and then dried to a constant dry weight in a ventilated oven at

Table 1

Leaf collection information of twelve bamboo species within two genera (*Phyllostachys* and *Pleioblastus*) from the Nanjing Forestry University campus, Nanjing, Jiangsu Province, P.R. China ($32^\circ 4' 47''\text{N}$, $118^\circ 49' 2''\text{E}$).

| Data set code | Scientific name | Sampling date | Sample size |
|---------------|---|---------------|-------------|
| 1 | <i>Phyllostachys aureosulcata</i> f. <i>spectabilis</i> C.D. Chu et C.S. Chao | 13 June 2018 | 308 |
| 2 | <i>Phyllostachys bambusoides</i> f. <i>castillonis</i> (Mitford) Muroi | 10 June 2018 | 310 |
| 3 | <i>Phyllostachys bambusoides</i> f. <i>lacrimadeae</i> Keng f. et Wen | 3 June 2018 | 323 |
| 4 | <i>Phyllostachys bisetii</i> McClure | 21 June 2018 | 312 |
| 5 | <i>Phyllostachys iridescens</i> C. Y. Yao et S. Y. Chen | 12 June 2018 | 294 |
| 6 | <i>Phyllostachys propinqua</i> McClure | 19 June 2018 | 310 |
| 7 | <i>Pleioblastus argenteostriatus</i> (Regel) Nakai | 26 May 2018 | 308 |
| 8 | <i>Pleioblastus chino</i> (Franchet et Savatier) Makino | 5 May 2018 | 514 |
| 9 | <i>Pleioblastus fortunei</i> (Van Houtte) Nakai | 15 June 2018 | 298 |
| 10 | <i>Pleioblastus maculatus</i> (McClure) C.D. Chu & C.S. Chao | 30 May 2018 | 292 |
| 11 | <i>Pleioblastus</i> sp. | 29 May 2018 | 263 |
| 12 | <i>Pleioblastus viridistriatus</i> (Regel) Makino | 5 June 2018 | 264 |

80 °C for at least 72 h. Leaf fresh and dry weights were both measured using an electronic balance (ME204/02, Mettler Toledo Company, Greifensee, Switzerland; measurement accuracy 0.0001 g).

2.3. Statistical methods

To stabilize the variance of the response variable, the data were log-transformed and fit to the equation

$$y = \gamma + \alpha x \quad (1)$$

Where y is the log-transformed leaf fresh or dry weight, γ is the normalization constant, α is the scaling exponent, and x is the log-transformed leaf area. Reduced major axis (RMA) regression protocols were used to fit the data to this equation (see Niklas, 1994; Niklas et al., 2007; Milla and Reich, 2007; Smith, 2009). The bootstrap percentile method was used to compare the numerical values of the scaling exponents (DiCiccio and Efron, 1996; Efron and Tibshirani, 1993; Sandhu et al., 2011). The 95% confidence intervals of γ and α were also calculated using the bootstrap percentile method. Additionally, Tukey's Honestly Significant Difference test with 0.05 significance level (Hsu, 1996) was used to determine the significance of differences in the quotients of leaf DW and FW (i.e., DW/FW) and that of leaf width (W) and length (L) (i.e., W/L) for the 12 bamboo species.

All statistical analyses were performed using the software R (version 3.2.2; R Core Team, 2015).

3. Results

As expected owing to the water content, the data revealed significant differences in the quotient of DW to FW among the 12 bamboo species ($p < 0.05$) (Fig. 1a and b and Table S1 in the online supplementary data). The DW/FW quotients of some species in the genus *Phyllostachys* (e.g., *Ph. bambusoides* f. *lacrimadeae*, *Ph. iridescens* and *Ph. propinqua*) were higher than species in the genus *Pleioblastus*. The median DW/FW of the *Phyllostachys* species fell into the 0.40–0.50 range, whereas those of the *Pleioblastus* species fell into the 0.35–0.45 range, i.e., the leaves of *Pleioblastus* species generally have higher water contents than those of *Phyllostachys* species.

Fig. 2 and Table S2 in the online supplementary data show the fitted results at the individual species level for the linearized relationship between DW and FW. The coefficients of determination exceeded 0.90 for each of the 12 species (with $r^2 > 0.96$ for 9 of the species), i.e., there is a strong positive relationship between DW and FW. There were 6 species whose 95% confidence intervals (CIs) of the scaling exponent included unity (i.e., $\alpha = 1.0$) and 6 species for which the 95% CIs do not (Table S2), i.e., increases in leaf water content for 6 out of the 12 species kept pace with increases of DW, whereas the remaining 6 species manifested significant allometric relationships.

The scaling relationship for FW vs. A was statistically robust for each of the 12 species investigated, and the lower bound of the 95% CIs of the scaling exponent exceeded unity for each the 12 species (Fig. 3 and Table S3 in the online supplementary data). With the exception of *Ph. bambusoides* f. *castillonis* (species code 2), the coefficients of determination of all species exceeded 0.90. For each species, the numerical value of the scaling exponent of FW vs. A exceeded unity, and thereby was consistent with the hypothesis of “diminishing returns” (Fig. 3). The same was also true for the scaling exponent of DW vs. A (Fig. 4). However, the coefficients of determination of the DW vs. A scaling relationship were lower than those of the FW vs. A scaling relationship for each species (compare Tables S3 and S4).

Scaling relationships between DW and FW, between FW and A, and between DW and A were evident at the genus level as well as at the species level (Fig. 5). The scaling exponent of the DW vs. FW scaling relationship for the pooled data from *Phyllostachys* was 1.060. The 95% CIs did not include unity (Fig. 5a). For the pooled data from *Pleioblastus*, the scaling exponent was 1.043 (with 95% CI = 1.032, 1.052) (Fig. 5b). Thus, at the genus level, DW is approximately proportional to FW, i.e., leaf water content approximately keeps pace with leaf weight. In addition, the scaling exponents of FW vs. A for the pooled data

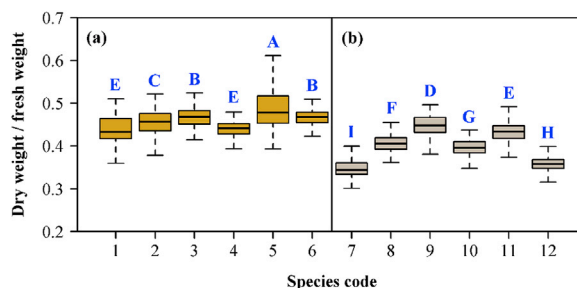


Fig. 1. Comparison of the quotients of leaf dry weight and fresh weight among 12 bamboo species within two genera: (a) *Phyllostachys* and (b) *Pleioblastus*. The letters on the boxes are used to show the significance of difference at $P < 0.05$. Species code: 1 = *Ph. aureosulcata* f. *spectabilis*, 2 = *Ph. bambusoides* f. *castillonis*, 3 = *Ph. bambusoides* f. *lacrimadeae*, 4 = *Ph. bissetii*, 5 = *Ph. iridescens*, 6 = *Ph. propinqua*, 7 = *Pl. argenteostriatus*, 8 = *Pl. chino*, 9 = *Pl. fortunei*, 10 = *Pl. maculatus*, 11 = *Pleioblastus* sp., 12 = *Pl. viridistriatus*. The letters above the upper whiskers are used to show the significance of the difference between any two species.

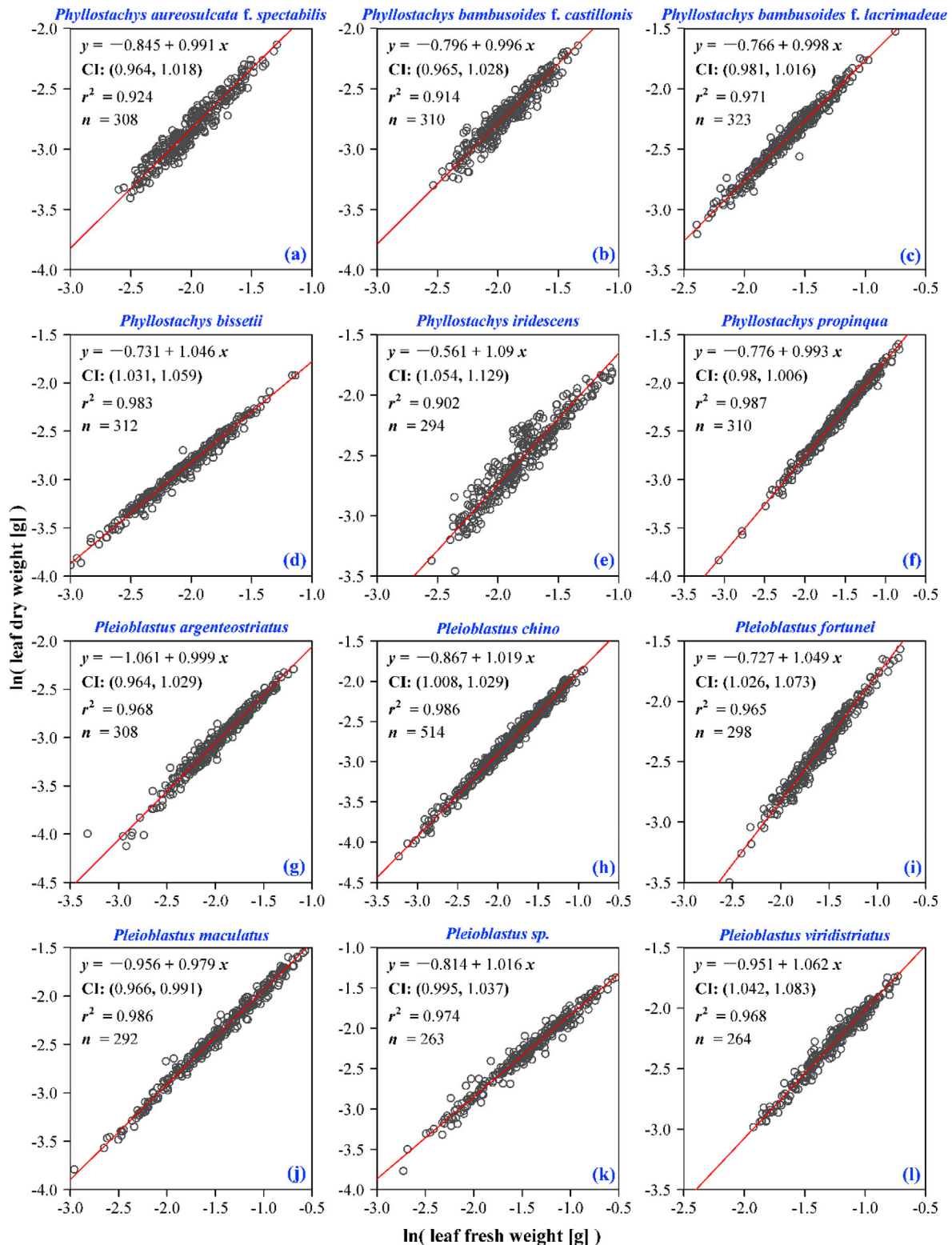


Fig. 2. Fit to the linearized relationship between leaf dry weight and fresh weight. Panels (a–l) represent different species. y is the predicted $\ln(\text{leaf dry weight})$ at $x = \ln(\text{leaf fresh weight})$; CI represents the 95% confidence interval of the slope; r^2 is the coefficient of determination that is used to indicate the goodness of fit of the linear fitting; and n represents the sample size, namely the number of sampled leaves.

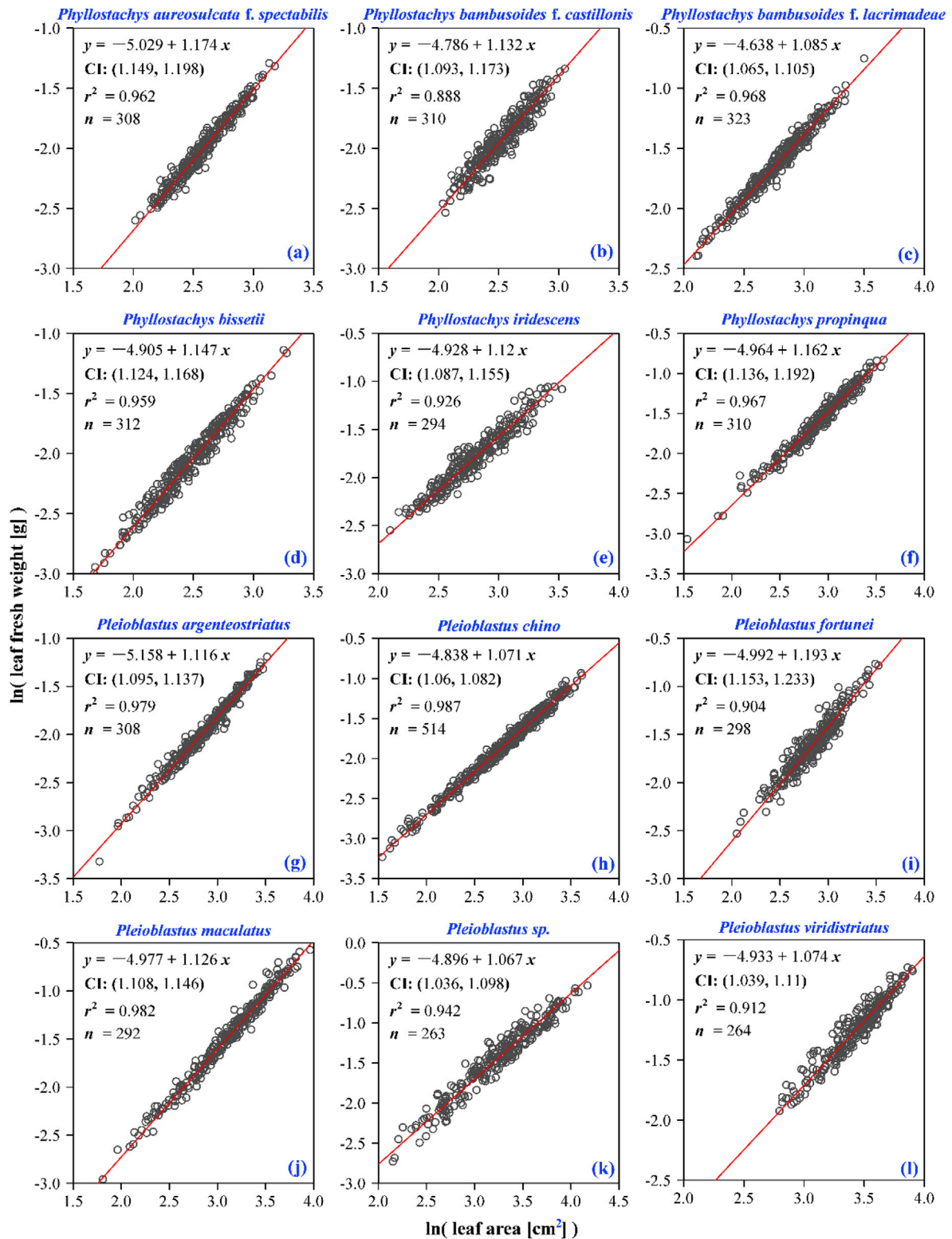


Fig. 3. Fit to the linearized relationship between leaf fresh weight and leaf surface area. Panels (a–l) represent different species. y is the predicted $\ln(\text{leaf fresh weight})$ at $x = \ln(\text{leaf surface area})$; CI represents the 95% confidence interval of the slope; r^2 is the coefficient of determination that is used to indicate the goodness of fit of the linear fitting; and n represents the sample size, namely the number of sampled leaves.

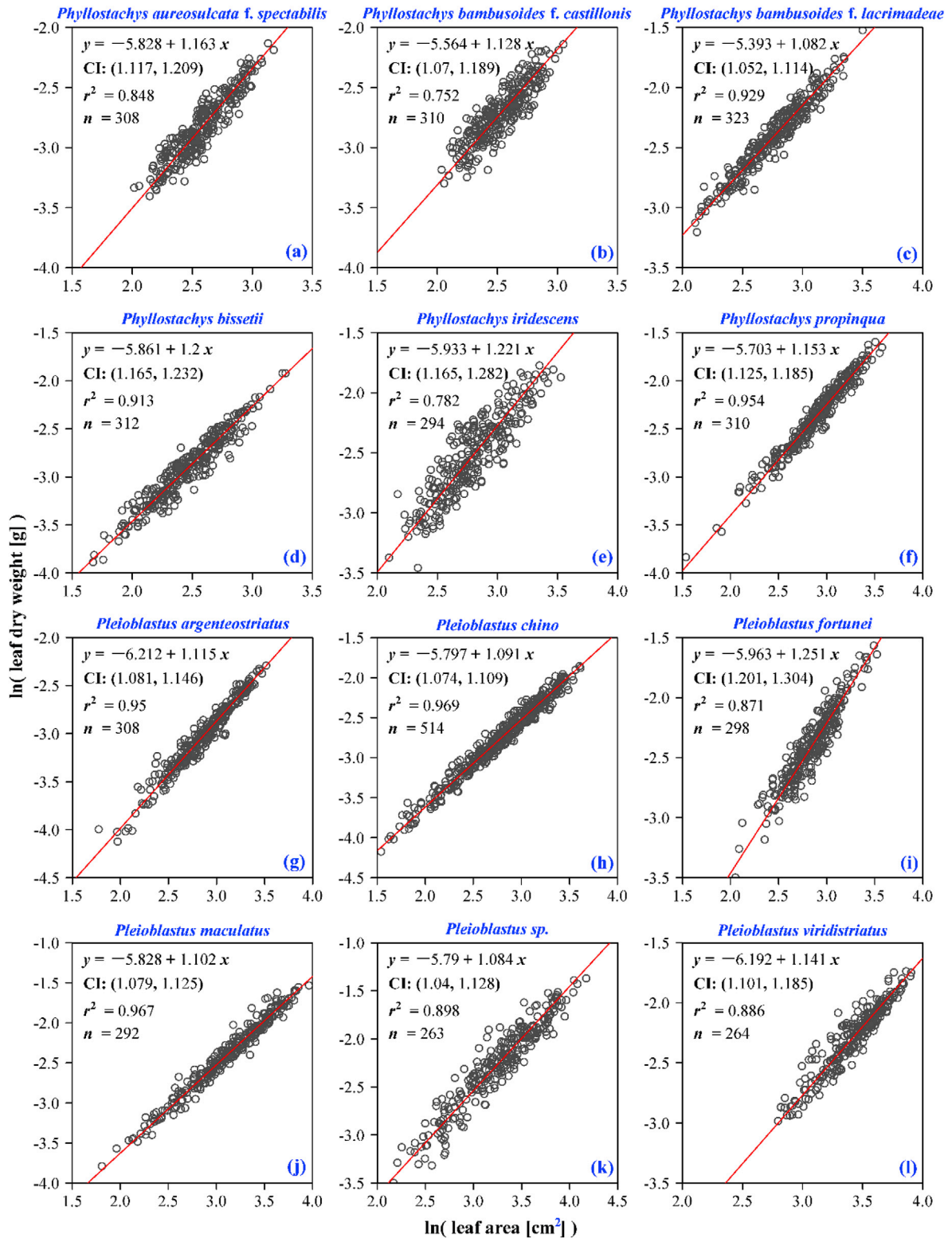


Fig. 4. Fit to the linearized relationship between leaf dry weight and leaf surface area. Panels (a–l) represent different species. y is the predicted $\ln(\text{leaf dry weight})$ at $x = \ln(\text{leaf surface area})$; CI represents the 95% confidence interval of the slope; r^2 is the coefficient of determination that is used to indicate the goodness of fit of the linear fitting; and n represents the sample size, namely the number of sampled leaves.

from *Phyllostachys* and the pooled data from *Pleioblastus* were both significantly greater than unity (Fig. 5c and d). Because the 95% CIs of the scaling exponents of the two genera did not overlap, the difference in the scaling exponents of the two genera was significant. Yet, once again, the numerical values of the two scaling exponents complied with the hypothesis of “diminishing returns”. The estimate of the scaling exponent of leaf dry weight vs. area is significantly greater than that of leaf fresh weight vs. area for each of the two genera (Fig. 5e and f).

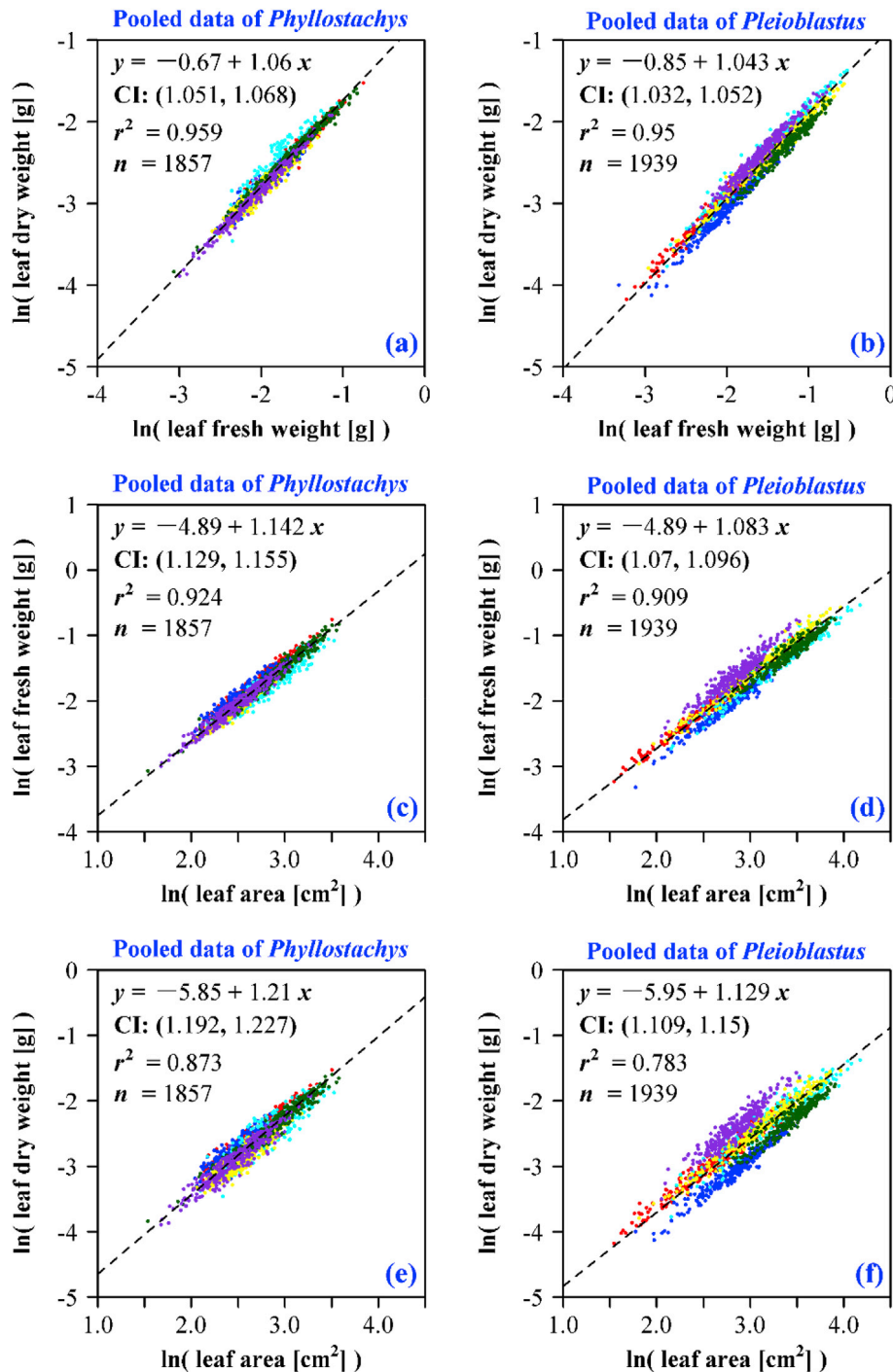


Fig. 5. Fit to the linearized scaling relationships between leaf dry weight and leaf fresh weight, between leaf fresh weight and leaf surface area, and between leaf dry weight and leaf surface area for the pooled data sets. Panels (a,c,e) represent the pooled data of *Phyllostachys*, and panels (b,d,f) represent the pooled data of *Pleioblastus*. y is the dependent variable, and x is the corresponding independent variable; CI represents the 95% confidence interval of the slope; r^2 is the coefficient of determination that is used to indicate the goodness of fit of the linear fitting; and n represents the sample size, namely the number of sampled leaves.

Finally, leaf *W/L* quotients of most *Phyllostachys* species were larger than those of most *Pleioblastus* species (Fig. 6a and b and Table S5 in the online supplementary data). Among the 12 bamboo species studied, *Ph. bambusoides* f. *castillonis* and *Ph. bissetii* (species 2 and 4, respectively) have the largest quotient of leaf width and length.

4. Discussion

The data presented here reveal three general trends both at the individual species level and when the data from each of two genera (*Phyllostachys* and *Pleioblastus*) are pooled: (1) the scaling relationship between leaf (lamina) fresh weight vs. lamina area manifests a better fit (as gauged by r^2 -values) than the scaling relationship between leaf dry weight vs. lamina area, (2) in general, the scaling of dry weight with respect to fresh weight is either isometric (a one-to-one scaling relationship) or allometric (with a scaling exponent that exceeds one), and (3) the phenomenon called “diminishing returns” is evident in the majority of cases (i.e., increases in lamina area fail to keep pace with increases in lamina dry weight). Each of these three observations is discussed in the following sections.

4.1. Fresh versus dry weight

If leaf water content were perfectly proportional to leaf dry weight, leaf fresh weight would also be proportional to leaf dry weight. The scaling exponent of leaf fresh weight vs. area would then be equal to that of leaf dry weight vs. area, and investigations regarding differences in the scaling exponents between these two leaf biomass measures would be meaningless. However, the data presented here for bamboo show that this is not the case. Although the scaling exponent of leaf dry weight vs. fresh weight approaches unity, 6 out of the 12 bamboo species (50%) had 95% confidence intervals that did not include unity (Table S2) and each of the remaining 6 species whose 95% CIs included unity showed non-significant differences between the scaling exponent of leaf fresh weight vs. area and that of leaf dry weight vs. area (Tables S2–S4). Comparing the fitted scaling relationship of leaf fresh weight vs. area with that of leaf dry weight vs. area, the data from several species (e.g., *Ph. bambusoides* f. *castillonis* and *Ph. iridescens*) deviate wildly from the fitted regression curve (Fig. 4), which might lead to an inaccurate estimate of the scaling exponent of leaf dry weight vs. area. In general, it appears that leaf fresh weight is a better predictor than leaf dry weight when developing a scaling relationship for leaf surface area (Fig. 3).

4.2. Leaf fresh weight, water content, and lamina area

Across all vascular plants, the scaling relationship between leaf fresh weight vs. leaf area is likely dependent upon the extent to which leaf growth is dependent upon water content and carbon allocation, and the extent to which carbon is allocated to lamina thickness versus surface area. The proportion of carbon allocated to leaf thickness versus leaf area is likely a tradeoff and dependent on ambient light conditions (White and Montes, 2005; Jullien et al., 2009). For example, in general, plants with thick leaves commonly grow in sunny habitats, whereas plants with thin leaves tend to occupy shady habitats (Evans and Poorter, 2001; Lambers et al., 2008; March and Clark, 2011; Wei et al., 2019). Thicker leaves with either longer palisade cells or multiple palisade cell layers are reported to have an enhanced capacity for what has been called “area-based” photosynthesis (Mitchell et al., 1999; Lambers et al., 2008). In the case of bamboo, Lin et al. (2018) report a $-3/4$ power-law relationship between leaf mean thickness and leaf area for 11 species.

4.3. Leaf shape

Leaf shape is correlated with venation patterns across many species (Runions et al., 2005, 2017). Across leaves with hierarchical dendritic venation patterns, an increase in the area of a narrow leaf tends to require a greater investment of dry

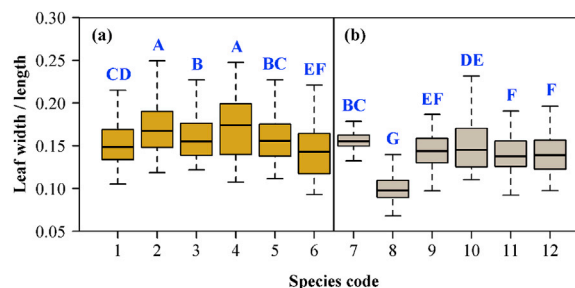


Fig. 6. Comparison of the quotients of leaf width and length among 12 bamboo species within two genera: (a) *Phyllostachys* and (b) *Pleiblastus*. The letters on the boxes are used to show the significance of difference at $P < 0.05$. Species code: 1 = *Ph. aureosulcata* f. *spectabilis*, 2 = *Ph. bambusoides* f. *castillonis*, 3 = *Ph. bambusoides* f. *lacrimadeae*, 4 = *Ph. bissetii*, 5 = *Ph. iridescens*, 6 = *Ph. propinqua*, 7 = *Pl. argenteostriatus*, 8 = *Pl. chino*, 9 = *Pl. fortunei*, 10 = *Pl. maculatus*, 11 = *Pleiblastus* sp., 12 = *Pl. viridistriatus*. The letters above the upper whiskers are used to show the significance of the difference between any two species.

matter than that for a broad leaf, because narrow leaves require a greater investment in dry matter in the first and secondary veins to maintain the transport of water and nutrients both from the main vein to the leaf margin and from leaf base to the tip (Roth-Nebelsick et al., 2001). In addition, narrow leaves with hierarchical venation patterns require a greater carbon investment than broad leaves to resist wind damage.

In contrast, as leaves with parallel venation patterns, such as bamboo, become narrower, they require more carbon investment in mid-veins (Niinemets et al., 2007; Su et al., 2019a). Thus, broad leaves can and do manifest numerically smaller scaling exponents for leaf biomass vs. area compared to narrow leaves, which tend to have higher scaling exponents. Shi et al. (2015) found that the bamboo with the broadest leaves (i.e., *Indocalamus victorialis* P. C. Keng) had the largest scaling exponent of leaf fresh weight vs. leaf surface area among four species of the genus *Indocalamus*. Using an extensive database involving 100 leaves from each of 101 bamboo species and cultivars, Lin et al. (2019) found that leaf shape (as defined by lamina width divided by lamina length) had a demonstrable effect on the scaling exponent of leaf dry weight vs. surface area, i.e., the scaling exponent for leaf dry weight vs. leaf surface area decreased towards unity with increasing width/length ratios. That is, the smaller the quotient of leaf width and length, the greater the scaling exponent of leaf dry weight vs. leaf area. However, our individual data and pooled data at a genus level do not confirm this trend. The leaves of *Phyllostachys* species with greater quotients of leaf width and length have numerically greater scaling exponents for the leaf fresh weight (or dry weight) vs. area relationship compared to the leaves of *Pleioblastus* species with smaller quotients of leaf width and length (Figs. 5 and 6).

This study provides a new result relative to our previous reports in Huang et al. (2019). In the previous study, we only demonstrated that the scaling relationship between leaf fresh weight and area is stronger than that between leaf dry weight and area. However, we did not recognize that whether the scaling exponent of leaf fresh weight vs. area is equal to that of leaf dry weight vs. area relies on whether leaf fresh weight is proportional to leaf dry weight. In the present study, we demonstrated this hypothesis. A proportional relationship between the two leaf biomass measures can result in a nonsignificant difference between the two scaling exponents; however, an allometric relationship between them will lead to a significant difference between the two scaling exponents.

5. Conclusions

The data presented for each of 12 bamboo species and the data pooled from each of the two genera examined in the present study indicate that, on average, leaf fresh and dry weight manifest an isometric scaling relationship and that the scaling relationship between leaf fresh weight versus leaf area often has a higher correlation coefficient than the scaling relationship between leaf dry weight versus leaf area. In addition, the data are consistent with the hypothesis referred to as “diminishing returns”, wherein leaf area fails to increase in direct proportion with increases in leaf mass. There is also evidence that leaf scaling relationships are influenced by leaf shape (as defined by the quotient of lamina width and length). We interpret these data to indicate that leaf water content (as well as leaf shape) need to be considered when empirically and theoretically exploring leaf scaling relationships.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00793>.

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